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'Tagging Study'

Recent Migrations of the Sacramento–San Joaquin River Striped Bass Population[1]

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ABSTRACT

Migration patterns of striped bass (*Roccus saxatilis*) in the Sacramento-San Joaquin River system, California, are defined by tag returns from 18,300 tagged fish and angler catches from 1958 through 1964.

Larger adults migrated farther downstream than smaller ones, and most 3- and 4-year-old immature fish remain in the Bay Area during the spawning period. Fish tagged in the western and eastern Delta during the spring, in the western Delta during the fall, in the upper Sacramento River during the spring, and in San Pablo Bay during the fall all had similar migration patterns. The only general difference was each group had a distinctive migration to the Delta.

Migrations into San Francisco Bay and the Pacific Ocean were much greater in the late 1950's and early 1960's than in the early 1950's. Data on changes in the striped bass population and environment were insufficient to explain migration changes. Earlier conclusions regarding factors controlling seaward migration did not adequately explain migration variations between 1958 and 1964.

INTRODUCTION

Tagging in the early 1950's demonstrated that adult striped bass from the Sacramento–San Joaquin River population had a definite annual migratory pattern (Calhoun, 1952). There was a mass upstream fall migration to the fresh waters of the Sacramento–San Joaquin Delta, where the fish remained over winter. In the spring, they dispersed throughout the Delta and its tributaries to spawn. As spawning ended in May and early June, fish migrated downstream to spend the summer in brackish or salt water. During the summers of 1950 and 1951, the population was concentrated in San Pablo Bay and Carquinez Strait.

By 1958, changes in the fishery indicated that there had been important changes in the timing and extent of migrations, although the pattern remained similar. Returns from extensive tagging operations between 1958 and 1961 helped define these changes and migratory differences among the population's various components.

This paper describes results of the 1958–1961 tagging study and compares them with earlier findings. Supplementary information on migrations obtained from creel censuses is also included.

STUDY AREA AND STRIPED BASS

Almost all California striped bass live in the Sacramento–San Joaquin River system and adjacent areas of the Pacific Ocean. These two rivers and their tributaries drain California's Central Valley. The Sacramento River flows from the north and the San Joaquin River from the south to join near Pittsburg (Figure 1). From there they flow to the Pacific Ocean through Suisun Bay, Carquinez Strait, San Pablo Bay, and San Francisco Bay. Upstream from their junction there is a network of some 700 miles of channels which is known as the Delta. The Delta covers a triangular area bounded by Pittsburg, Sacramento, and Tracy.

From Sacramento and Tracy to the Pacific Ocean the area is a tidal estuary. Runoff is much greater in the winter and spring, causing wide variations in salinity intrusion from the ocean. Even in the late summer period of greatest salinity intrusion water is essentially fresh about 5 miles east of Antioch. Kelley (1966) describes the area in more detail.

Striped bass utilize the entire area. They spawn upstream from Pittsburg: mostly in the Delta portion of the main San Joaquin River and in the Sacramento River from the Delta to above the Feather River (Farley, 1967).

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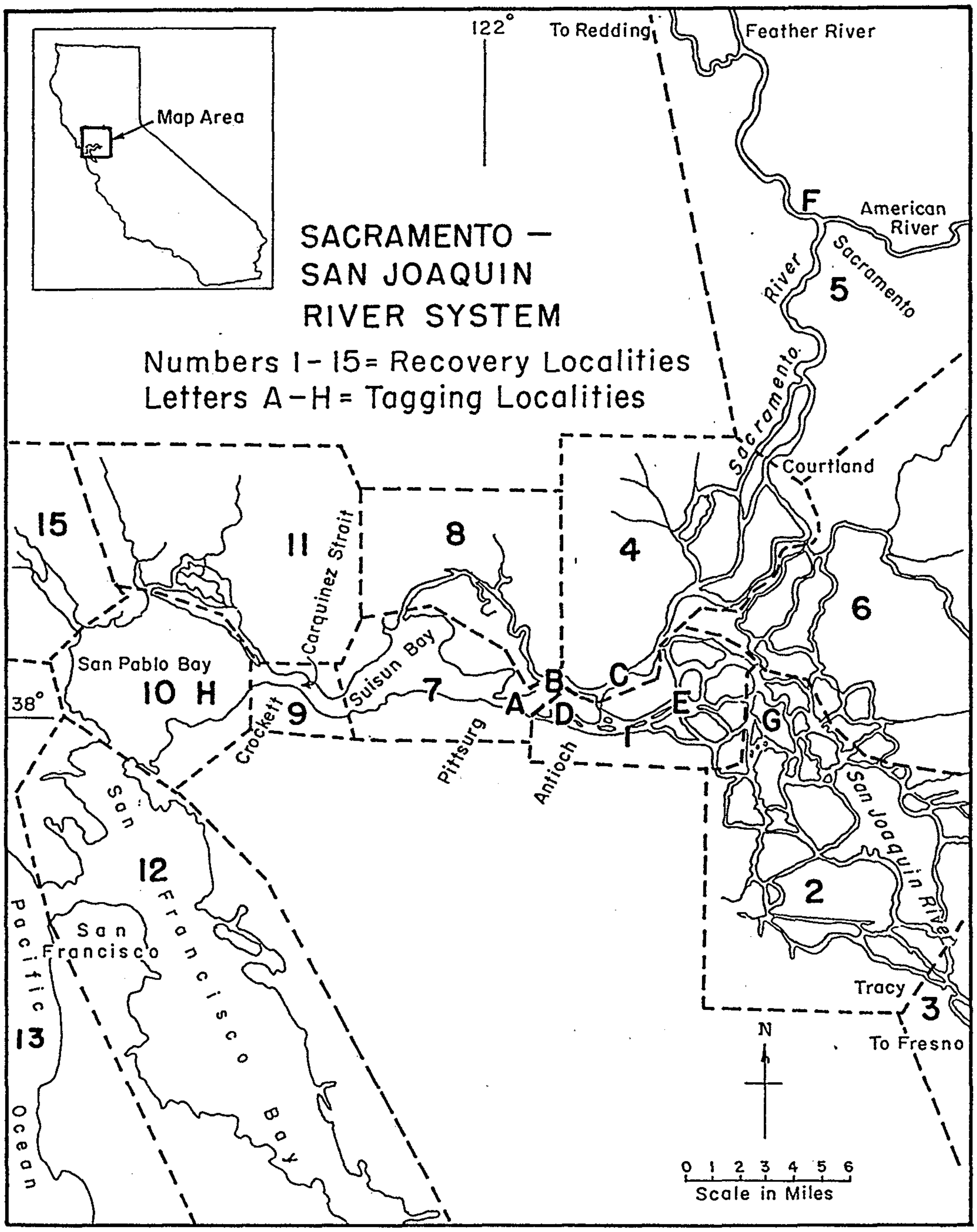


FIGURE 1.—Map of the study area showing the Sacramento River flowing from the north and the San Joaquin River from the south. They meet at Pittsburg and flow through a series of bays to the Pacific Ocean. The network of channels in the triangular area bounded by Pittsburg, Sacramento and Tracy is known as the Delta. Tagging sites are designated by letters. Recovery localities are designated by numbers and outlined by dashed lines.

Young fish utilize the area from San Pablo Bay upstream as a nursery area. As they mature at 2 to 5 years old, they take up adult migratory patterns and travel over the entire area.

METHODS

Description and evaluation

The main groups of striped bass were captured with drift gill nets and tagged in the western Sacramento–San Joaquin Delta each spring. This time and location was selected under the hypothesis that it would provide a representative sample of the mature population, since spawning occurs only in the spring, in the tagging area or upstream from it. All mature fish probably migrate through this area each spring.

Tagging was done at five locations in the western Delta. These were: Sacramento River at Chipps Island (A, Figure 1), Sacramento River at Chain Island (B, Figure 1), Sacramento River off entrance to Sherman Lake (C, Figure 1), Broad Slough (D, Figure 1), and San Joaquin River below False River (E, Figure 1). Throughout this paper fish tagged at these localities are designated as representative of the western Delta population.

Additional striped bass were caught for tagging in wire fyke nets (Hallock, Fry, and LaFaunce, 1957) at Fremont Weir in the upper Sacramento River (F, Figure 1) in May 1958, in gill nets at Prisoner's Point in the eastern San Joaquin Delta (G, Figure 1) in the spring of 1959, and by angling and gill netting in San Pablo Bay (H, Figure 1), and western Delta in the fall of 1958.

Since fishing gear and methods were somewhat selective the tagged sample does not represent the population exactly. Gill nets used in 1958 were multifilament nylon with six panels of equal length, ranging in stretched mesh size from 4½ to 7 inches by ½-inch increments. Nets used from 1959 to 1961 had eight panels, ranging from 4 to 7 inches plus an 8-inch panel.

Graduated mesh nets tend to catch various sizes of fish randomly, but several biases exist. In this study the panels were arranged in order by size, and the end with the largest mesh was usually laid out first and picked up last to avoid excessive catches of smaller fish in the smaller mesh sections. Moreover, striped bass frequently catch their maxillaries in mesh too small to gill them, but few bass are caught in mesh too large to gill them. A third important bias is that the thicker net twine used in the larger meshes makes them less efficient. While the last item counteracts the first two, the first two were probably more important, biasing the sample towards catching larger fish.

Most bass were tagged with disk dangler tags, although other tags were used for evaluation purposes (Chadwick, 1963). Also, 150 to 400 of each spring's 1,943 to 4,378 disk dangler tags were reward tags. While these different tags affected recovery rates, they are ignored in this paper as they are unimportant in interpreting migration patterns.

Only legal-sized fish were tagged (16 inches or over total length). Fork length was measured to the nearest inch.

To identify which tagged fish, recaptured more than 1 year after tagging, were 25+ inches long, growth of tagged fish was approximated from recent growth data (Robinson, 1960). All those 22 to 24 inches long at tagging were assumed to be at least 25 inches long one year after tagging; those 18 to 21 inches long at tagging were assumed to be at least 25 inches long two years after tagging; and all tagged fish were assumed to be at least 25 inches long three years after tagging. This rough approximation ignores evidence of slower growth of tagged fish (Chadwick, 1963).

In 1960 and 1961 each individual was sexed externally. Those from which milt could be expressed were recorded as males. Others were assumed to be females. Internal examination of fish initially sexed externally showed that about 95% of the males present in the Delta during the tagging period could be sexed correctly by external examination.

Fish tagged in the western Delta (A through E, Figure 1) were initially stratified by size, sex, and tagging area and time. The effect of each of these on migrations was examined by comparing the proportional distribution of first-year recoveries among geographical areas (Figure 1) and months. No statistical test is available to determine the significance of geographical and seasonal differences simultaneously. Hence, they were analyzed independently by chi-square tests. This is a rather inefficient statistical procedure. Many samples were small, so only rather gross differences could be detected. The number of strata were reduced by grouping areas and months to obtain expected values larger than five in most cells to satisfy sample size requirements for chi-square tests.

Defining migrations from tag returns has inherent limitations, since returns reflect angler harvest, which is affected by many things besides the presence of fish. For striped bass the most important probably are:

1) Seasonal changes in feeding habits—striped bass are relatively invulnerable during the spawning season and during the winter when their feeding is much reduced.
2) Weather—Strong winds frequently make fishing impossible. Prevailing west winds during the summer particularly limit fishing in San Pablo Bay.
   The time rain starts in the fall can also be important as rain inhibits fishing. For example, the good fall fishing in the Delta in 1958 probably resulted from warm rainless weather extending through December.
3) Availability of boating facilities—Most anglers fish within a few miles of boat launching or berthing facilities. The relative scarcity of these facilities in the Suisun Bay area reduces angling there, even though most adults migrate through the area twice a year and many winter there.
4) Water turbidity—Turbidity is greater in the Delta than in bay areas, probably making angling less effective in the Delta.
5) Changes in fishing techniques—These will be discussed later.

In addition, while in the ocean, striped bass are caught chiefly in the surf. They may well occur elsewhere in the ocean but be invulnerable. In this case, tag returns would reflect ocean migrations poorly.

TABLE 1.—*Summary of striped bass tagging*

Tag group	Tagging localities*	Tagging dates	Number tagged	Mean fork length (inches)
Spring tagging				
Western Delta 1958	B through E	11 April–5 June	4,378	22.1
Western Delta 1959	A through E	6 May–11 June	4,262	21.7
Western Delta 1960	A through E	6 April–2 June	4,317	22.6
Western Delta 1961	B through E	8 April–23 May	1,943	23.1
Fremont Weir 1958	F	29 April–20 May	890	19.0
Eastern Delta 1959	G	15 April–9 June	1,146	22.9
Fall tagging				
San Pablo Bay 1958	H	26 Sept.–13 Nov.	750	18.7
Western Delta 1958	A through E	6 Oct.–4 Dec.	628	23.2

* Letters refer to localities in Figure 1.

The importance of these factors and possibly others cannot be measured quantitatively, making the assessment of annual differences in returns difficult. These factors have less effect on the assessment of differences among various groups within any given year.

While tag returns from this study are very useful for showing long-term trends and differences in migratory patterns, returns were too few to show short-term differences well.

Supplementary information on the migrations of males and females was obtained from observations of sex composition of the angler catch in the Delta during the spring of 1961 and 1962 and in San Francisco Bay in the spring of 1961. Gonads of all fish, except ripe males, were examined (Chadwick, 1965).

Western Delta spring population

Description of tagged population.—In the springs of 1958–1961, 14,900 striped bass were tagged in the western Delta (Table 1). Mean lengths for each year's group were similar.

Few small females were caught. Only 10 and 6% of the females tagged in 1960 and 1961 were less than 22 inches FL, but 49 and 47% of the males tagged were less than 22 inches. As a result, approximately 73 and 64% of the bass tagged in 1960 and 1961 were males. Respective mean fork lengths were 21.6 and 21.7 inches for males and 25.2 and 25.5 inches for females.

TABLE 2.—*Results of Chi-Square tests to determine whether tagging area, tagging time, fish length, or sex affected area or time of recovery significantly*[1]

	Tests for differences in recovery area				Tests for differences in recovery time			
Tag group	Tagging locality	Tagging time	Length group	Sex	Tagging locality	Tagging time	Length group	Sex
1958	0.40	0.03	<0.001		0.48	0.30	<0.001	
1959	0.09	0.23	<0.001		0.62	0.053	<0.001	
1960	0.74	0.93	<0.001	0.004	0.82	0.15	0.19	0.55
1961	0.79	0.23	0.02	0.60	0.85	0.13	0.28	0.92

[1] Values in table are the approximate probabilities of obtaining a larger χ^2 value by chance. Only first year returns are included.

General results

About 4,600 or 31% of these tags were returned through the spring of 1964. It is necessary to understand how tagging locality, time of tagging, length of fish, and sex affect returns before migrations can be interpreted, so these are examined first.

Effect of population characteristics on migrations

Geographical components.—Tagging locality within the western Delta did not significantly affect the time or place of recapture (Table 2). The only appreciable departures from expected proportions were returns from the San Joaquin River and adjacent sloughs in 1958 and 1959. In those years, 17.3 and 12.4% of the returns from bass tagged in the San Joaquin River at location E were recovered in the San Joaquin Delta, while only 7.8 and 6.5% of the returns from fish tagged in the Sacramento River at locality C were recovered there. This difference did not occur in 1960 and 1961, nor did the returns from the Sacramento River show any appreciable deviations from expected proportions. This leads to the conclusion that striped bass migrating through various portions of the western Delta in the spring migrate similarly, so tagging localities within this area can be ignored in analyzing migrations.

Time of occurrence in Delta.—To determine whether striped bass occurring in the Delta at different times had similar migration patterns, tagged fish were divided into the following five groups by time of tagging: Before 20 April, 20–30 April, 1–15 May, 16–31 May, and June. Returns differed significantly in place of recovery only in 1958, and returns did not differ significantly in time of recovery in any year (Table 2). The small differences observed showed no consistent trend. Hence striped bass occurring in the Delta at different times in the spring also migrate similarly, so time of tagging can be ignored.

TABLE 3.—*Relationships between fish length and migration pattern based on first year returns from striped bass tagged in the Western Delta in springs of 1958–1961*

Recovery locality[1]	Percentage returns by length groups (inches) 15–20	21–24	25+
Upper San Joaquin River (3)	0.1	0.0	0.0
Eastern San Joaquin Delta (2)	1.7	1.9	1.9
Mokelumne River and Delta (6)	1.0	0.7	0.6
Western San Joaquin Delta (1)	6.6	7.1	8.6
Upper Sacramento River (5)	7.1	6.3	4.9
Lower Sacramento River (4)	10.1	7.2	7.0
Suisin Bay Area (7)	7.5	4.3	6.0
Montezuma Slough Area (8)	0.7	1.1	0.7
Carquinez Strait (9)	7.7	5.6	4.3
Napa River (11)	4.4	2.9	4.4
San Pablo Bay (10)	18.1	12.7	11.3
Petaluma Creek Area (15)	0.1	0.3	0.4
San Francisco Bay (12)	32.1	44.4	33.0
Pacific Ocean (13)	2.8	5.6	16.9

[1] Numbers in parentheses refer to recovery locations designated in Figure 1.

Length groups in lower Delta.—Tagged fish were divided into three length groups: 15 to 20 inches FL, 21 to 24 inches, and 25 inches and larger. Returns differed significantly in place of recovery in all years and in time of recovery in 1958 and 1959 (Table 2). This clearly indicates different sized striped bass migrate differently.

The greatest difference among the three groups was that larger fish moved farther downstream. Returns from Carquinez Strait–San Pablo Bay were highest for 15- to 20-inch individuals, those from San Francisco Bay were highest for 21- to 24-inch fish, and those from the Pacific Ocean were highest for 25-inch and larger fish (Table 3). These differences were consistent in all years, except that the San Pablo Bay returns in 1960 and 1961 were similar for all groups.

In addition, returns from the Sacramento River were generally higher for small than larger fish. Deviations from expected χ^2 values were relatively small, but they were consistent for the smallest and largest size groups, except for 25+ inch fish in 1961.

TABLE 4.—*Percentage of males in spring samples from the Sacramento-San Joaquin Delta*

Date	1960	1961		1962
	Gill net	Gill net	Angler caught	Angler caught
1–30 March			76	87
1–15 April	76	91	70	74
16–30 April	73	46	46	49
1–15 May	70	63	53	57
16–31 May	75	50	78	72
Seasonal total	73	64	59	66

Sex.—Place of recovery differed significantly for males and females in 1960, but not in 1961 (Table 2). Time of recovery did not differ significantly in either year (Table 2).

Since the average size of males in the tagged sample was smaller than the average size of females, the effects of length and sex were confounded in these results. An attempt was made to separate them by comparing migratory patterns of different size groups of each sex, and by comparing migratory patterns of each sex within each size group. Small sample sizes caused inconclusive results, however.

Since deviations from expected χ^2 values were smaller for sex than for length, it is probable that size was the primary controlling factor. However, additional data are needed to confirm this.

While tag returns did not indicate important differences in migratory patterns for males and females, the sex composition of the tagged population itself suggested important differences associated with sex. As previously mentioned, 73 and 64% of the striped bass tagged in 1960 and 1961 were ripe males. Over half of those caught by anglers in the spring were also males (Table 4). Thus, males were more abundant than females in the Delta during the spring. Essentially all bass observed there were mature.

In contrast, 76% of 823 striped bass observed on nine days between 8 April and 24 June 1961, in the sport fishery in San Francisco and San Pablo bays were females. At least 40% of the females and 79% of the males observed there during April and May were immature. These data indicate that immature males and females did not migrate to the Delta, and since females mature later in life than males (Scofield, 1931), females dominated bay area catches during the spring.

TABLE 5.—*Summary of seasonal striped bass migrations from June 1958 through May 1962*

Locality**	Jun–Aug	Sep	Oct	Nov	Dec–Feb	Mar–May	Annual total
	Tag returns by months*						
Upper Sacramento River (5)	0.03	0.02	0.04	0.04	0.08	0.94	1.15
Upper San Joaquin River (3)	+	0	0	0	+	0	+
Delta (1, 2, 4 & 6)	0.15	0.10	0.31	0.62	0.57	1.08	2.83
Suisun Bay (7 & 8)	0.10	0.12	0.20	0.34	0.18	0.07	1.01
Carquinez Strait and Napa River (9 & 11)	0.51	0.26	0.26	0.22	0.15	0.07	1.47
San Pablo Bay (10 & 15)	0.47	0.34	0.68	0.32	0.16	0.18	2.15
San Francisco Bay (12)	2.64	0.85	0.86	0.50	1.07	0.38	6.30
Pacific Ocean (13)	0.85	0.20	0.12	0.04	0.01	0.02	1.24
Total	4.75	1.89	2.47	2.08	2.22	2.74	16.15

* Numbers are the mean percentages of numbers tagged. Only first-year returns from each year's tags were used. + indicates less than 0.05.

** Numbers in parentheses refer to recovery areas in Figure 1.

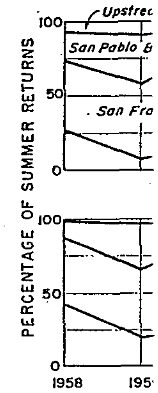
Mature females outnumbered mature males in the San Francisco and San Pablo Bay catches through the spring. Large numbers of spent females were present there by late May, while spent males did not appear in numbers until June, indicating that males probably spent more time on the spawning grounds than females. This would also contribute to the disproportionate sex ratio in both areas.

Annual migration patterns

General pattern.—During the summer, the vast majority of bass were downstream from Suisun Bay (Table 5). Most tag returns came from San Francisco Bay, but substantial numbers were taken in the Pacific Ocean and the Carquinez Strait–San Pablo Bay area. Virtually all tag returns upstream from these areas were either late downstream migrants caught in early June or early upstream migrants caught in late August.

Ocean returns ranged from the southern part of Monterey Bay to Tomales Bay, which are about 100 miles south and 45 miles north of the Golden Gate, respectively. Recoveries occurred as far offshore as 10 miles off San Francisco.

Fall tag returns demonstrated an upstream migration. San Francisco Bay and Pacific Ocean returns declined throughout the fall; Carquinez Strait–San Pablo Bay area returns



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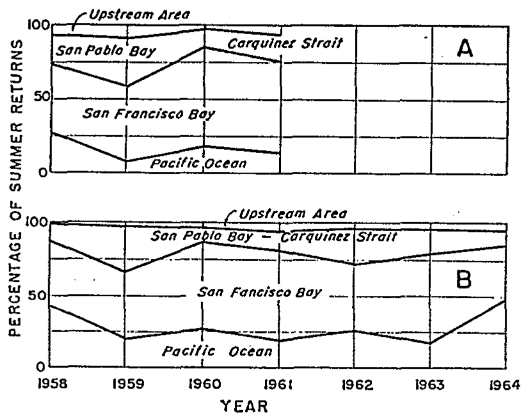

FIGURE 2.—Annual variations in summer striped bass migrations based on: A, first year returns from western Delta fish tagged during the spring; B, returns from western Delta tagged fish which were estimated to be 25 inches or larger when captured.

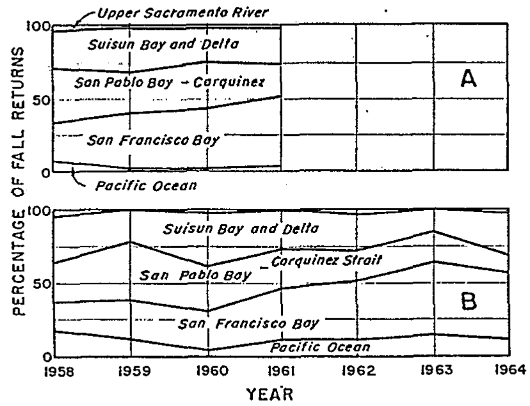

FIGURE 3.—Annual variations in fall striped bass migrations based on: A, first year returns from western Delta fish tagged during the spring; B, returns from western Delta fish tagged during the spring which were estimated to be 25 inches or larger when captured.

peaked in October and declined in November; and Delta and Suisun Bay returns increased to a peak in November. Very few bass were caught in the upper Sacramento River during the fall.

During the winter, fish were caught regularly in all areas from the Delta to San Francisco Bay. The largest number of returns were from San Francisco Bay, indicating that a substantial population probably winters there.

During the spring, most fish were in the Delta or upper Sacramento River. In both areas, but particularly in the upper Sacramento River, returns reached their annual peak. Returns from all downstream areas were low. San Pablo Bay returns increased slightly over winter returns, reflecting an early spring fishery in the western part of this Bay.

Very few striped bass were caught in the upper San Joaquin River between 1958 and 1964.

Variations in annual migrations.—Annual tag return patterns differ substantially. A chi-square test of the hypothesis that the proportion of each year's returns coming from each recovery locality was constant rejects the hypothesis at the 99.9% level ($\chi^2 = 321.1$; $\chi^2_{.999,\ 45\ \mathrm{d.f.}} = 80.0$). However, these differences reflect both migration differences and changes in the fishery caused by factors which are either independent of migrations or give a biased measure of migrations. Some of these factors are discussed in the Methods section. There is no quantitative way of differentiating effects from these sources.

Summer distributions (June through August) varied appreciably (Figures 2a and b). Variations were similar for the whole population and for 25+ inch fish, but the larger fish were usually located farther downstream. Migrations into the Pacific Ocean were greatest in 1958 and 1964. The population was located farthest upstream in 1959, and it was concentrated most heavily in San Francisco Bay in 1960, 1961, and 1963.

During the fall (September through November) of 1958 through 1961, the whole population and the larger fish migrated somewhat differently (Figures 3a and b). The fraction of the whole population caught in San Francisco Bay increased steadily; in San Pablo Bay it declined steadily, and in Suisun Bay and the Delta it remained constant. Returns of 25+ inch individuals differed in that the fraction from San Pablo Bay was greatest in 1959 instead of 1958, and Suisun Bay and Delta returns fluctuated appreciably. Over the seven-year span, the fraction of larger fish caught in San Francisco Bay gradually increased, the fraction caught in San Pablo

TABLE 6.—*Annual geographical distribution of tag returns from striped bass caught in the Pacific Ocean*

Location	Percentages of total annual ocean recoveries						
	1958	1959	1960	1961	1962	1963	1964
Marin County beaches	5	6	5	6	8	13	16
San Francisco beaches	47	69	53	32	43	30	14
San Mateo County beaches	27	16	25	58	29	47	59
Santa Cruz County and Monterey Bay beaches	19	6	5	3	15	2	0
Boats out of San Francisco	2	4	13	1	5	9	11
Number returned	129	51	106	69	65	47	37

Bay declined, and the fraction caught in Suisun Bay and the Delta fluctuated with a slight downward trend. Fall returns from the Ocean varied some but showed no trend.

These trends suggest that as the study period progressed the population tended to remain in San Francisco Bay longer in the fall, that fish migrated upstream through San Pablo Bay more rapidly in the fall, and that either the fraction going to the Delta decreased slightly, or the migration was delayed, or both. Returns from the Delta are too few to indicate the migration's timing precisely.

There were enough winter (December through February) tag returns to indicate the geographical distribution of the catch only in 1958, 1959, and 1960. In 1958, 50% of all winter returns were from the Delta, almost another 25% were from Suisun Bay and the upper Sacramento River, and only 4% from San Francisco Bay. In marked contrast, 69 and 58% of the 1959 and 1960 winter returns were from San Francisco Bay. The few returns in subsequent years follow the 1959 and 1960 pattern.

These differences certainly reflect variations in the fishery, but they may not indicate migration changes. For example, the excellent 1958 Delta fishery at least partially reflects unusually good fishing weather. Moreover, true differences of this magnitude in winter distribution are unlikely, since fall distribution is relatively constant.

Except for 1959, 1960, and 1961, spring tag returns are also too limited to reflect the fishery. Twenty-four percent of the 1961 returns came from San Francisco Bay. This is about twice the 1959 and four times the 1960 percentages. Spring recoveries in the Delta were 50, 47, and 36% of the respective totals for the 3 years. Percentages from the upper Sacramento River were 20, 35, and 30 respectively.

Both the fraction of total returns which were from fish caught in the Pacific Ocean and the geographical (Table 6) and seasonal (Table 7) distributions of ocean returns varied from year to year. Surf fishermen along San Francisco and San Mateo county beaches were responsible for most ocean recaptures. The distribution within these two areas varied greatly and was not correlated with the extent of southward movement. Only in 1958 and 1962 were substantial numbers of striped bass caught south of San Mateo County.

Very few striped bass were caught north of the Golden Gate (Marin County), probably reflecting both the predominantly southern direction of movement and more limited fishing access north of the Gate. This fraction increased toward the end of the 1958–1964 period.

During this period of relatively great ocean migrations, no tagged fish were taken more

TABLE 7.—*Variations in timing of migrations to Pacific Ocean as indicated by tag returns*

Month recaptured	Percentages of total annual ocean recoveries[1]						
	June 1958–May 1959	June 1959–May 1960	June 1960–May 1961	June 1961–May 1962	June 1962–May 1963	June 1963–May 1964	June 1964–January 1965
June	12	27	18	14	2	17	5
July	28	29	44	26	38	30	19
August	17	14	27	30	29	21	59
September	19	22	8	25	29	21	16
October	16	4	3	0	2	11	0
November to May	9	4	0	4	0	0	0
Number returned	129	51	106	69	65	47	37

[1] Totals not always 100% result from rounding percentages.

TABLE 8.—*Comparison of July 1958 through June 1959 returns from 15–20 inch striped bass tagged in upper Sacramento River and Western Delta in spring of 1958*

Recovery locality*	Percentage of July through February returns: Upper Sacramento River tags	Percentage of July through February returns: Western Delta tags	Percentage of March through June returns: Upper Sacramento River tags	Percentage of March through June returns: Western Delta tags
San Joaquin Delta (1, 2, 3, 6)	12	10	18	23
Lower Sacramento River (4)	10	9	13	21
Upper Sacramento River (5)	4	1	61	23
Suisun Bay (7, 8)	10	5	2	1
Carquinez Strait (9)	9	10	3	3
San Pablo Bay (10 + 15)	26	29	2	8
Napa River (11)	9	7	0	5
San Francisco Bay (12)	18	24	2	15
Pacific Ocean (13)	2	7	0	1
Number of returns	104	242	62	75

* Numbers in parentheses refer to recovery areas defined in Figure 1.

TABLE 9.—*Comparison of first-year returns from striped bass tagged in Eastern San Joaquin Delta with those tagged in Western Delta in spring of 1959*

Recovery locality*	Percentage of June through October returns: Eastern Delta tags	Percentage of June through October returns: Western Delta tags	Percentage of November through May returns: Eastern Delta tags	Percentage of November through May returns: Western Delta tags
Eastern San Joaquin Delta (2, 6)	0	†	14	5
Western San Joaquin Delta (1)	2	2	15	12
Upper Sacramento River (5)	2	1	15	13
Lower Sacramento River (4)	2	4	10	13
Suisun Bay (7, 8)	6	8	10	7
Carquinez Strait (9)	9	9	3	3
San Pablo Bay (10, 15)	14	18	6	7
Napa River (11)	11	5	1	4
San Francisco Bay (12)	46	47	24	35
Pacific Ocean (13)	8	6	0	†
Number of returns	90	328	78	298

* Number in parentheses refer to recovery areas defined in Figure 1.
† Indicates a percentage between 0 and 0.5.

than 45 miles north of the Gate. This was noteworthy because striped bass stocks along the Oregon Coast must have originated from California migrants (Morgan and Gerlach, 1950).

Ocean returns were largely restricted to the surf except in 1960, when several tagged individuals were caught near the San Francisco lightship, about 10 miles off the California coast. None was caught this far off the coast in other years. Judging from fishermen's reports as well as these returns, there was a real difference in 1960 population distribution.

Ocean returns were largely confined to the period June through September (Table 7). Exceptions occurred in 1958 when many tagged striped bass were captured in October and a few through the winter, and in 1963 when 11% of the annual total recaptures was caught in October. Catches usually peaked in July. The only major exception occurred in 1964, when almost 60% of the fish were caught in August.

Other population components

Upper Sacramento River.—Striped bass tagged at Fremont Weir on the upper Sacramento River in the spring of 1958 were considerably smaller than those tagged in the Delta (Table 1). Fyke net size selectivity may have caused this difference, since the nets used were size selective for king salmon (*Oncorhynchus tshawytscha*) (Hallock, Fry, and LaFaunce, 1958). Because 76% were less than 21 inches long, only migrations of 15- to 20-inch Fremont Weir and western Delta bass were compared.

Migrations were similar for the two groups from July 1958 through February 1959, as recovery areas did not differ significantly ($x^2 = 12.2$; $x^2_{.95,\ 6\ d.f.} = 12.6$) (Table 8).

However, in the spring of 1959 a much higher percentage of the Fremont Weir population returned to the upper Sacramento River, giving clear evidence of strong homing by fish spawning in the upper Sacramento River. It is not known whether these are progeny of fish which spawned there, or whether they developed this pattern later in life.

homing

Eastern San Joaquin Delta.—Striped bass tagged at Prisoner's Point in the eastern San Joaquin Delta were somewhat larger than those tagged in the western Delta during the spring of 1959 (Table 1). Despite this size difference, returns from the two groups were similar, with the main difference occurring from November 1959 through May 1960, when western Delta fish were farther downstream (Table 9). The greatest difference was in returns from the eastern San Joaquin Delta. There the percentage for eastern Delta

TABLE 10.—*Comparison of returns from striped bass tagged in San Pablo Bay in the fall of 1958 and in the Western Delta in the spring of 1958*

Recovery locality*	Percentage of November through February returns		Percentage of March through May returns	
	San Pablo Bay tags	Western Delta tags	San Pablo Bay tags	Western Delta tags
San Joaquin Delta (1, 2, 6)	25	22	19	27
Sacramento River (4, 5)	14	27	19	42
Suisun Bay (7, 8)	5	11	2	4
Carquinez Strait and Napa River (9, 11)	6	12	8	4
San Pablo Bay (10)	42	17	28	8
San Francisco Bay (12)	8	9	24	12
Pacific Ocean (13)	0	2	0	2
Number of returns	85	278	90	156

* Numbers in parentheses refer to recovery areas defined in Figure 1.

bass was almost three times that for western Delta bass. Considering all first-year returns, areas of recovery differed significantly for the two groups ($\chi^2 = 18.4$; $\chi^2_{.95,\ 9\ d.f.} = 16.9$). Seventy-eight percent of this χ^2 value results from deviations from expected eastern Delta returns, confirming that striped bass tend to return to the same spawning area they used the previous year.

Western Delta fall population.—Striped bass tagged in the western Delta during the fall (mostly late November and early December) of 1958 were about the same size as those tagged there in the spring (Table 1). They could logically be assumed to represent the adult bass which migrate back to the Delta in the fall, overwinter there, and spawn before migrating downstream. Tags returned through February supported this, as all were recaptured upstream from Carquinez Strait. However, in March 1959 two returns were received from San Francisco Bay, two from San Pablo Bay, and eight from Delta areas. Since the two caught in San Francisco Bay were large enough to be mature, and since striped bass had never been found spawning this early in the Sacramento–San Joaquin system, these returns suggested that some mature bass migrate to the Delta in the fall, and move back to the Bay during the winter. Presumably, these would have returned to the Delta to spawn in the spring.

During April 1959, 16 of 39 returns from fish tagged in the fall in the western Delta were recaptured in areas downstream from

TABLE 11.—*Comparison of June through December 1959 returns from striped bass tagged in San Pablo Bay during the fall of 1958 and in the Western Delta during the spirng of 1959**

Recovery locality†	Percentage of San Pablo Bay tags	Percentage of Western Delta tags
San Joaquin Delta (1, 2, 6)	9	6
Sacramento River (4, 5)	13	6
Suisun Bay (7, 8)	7	11
Carquinez Strait & Napa River (9, 11)	18	13
San Pablo Bay (10, 15)	18	15
San Francisco Bay (12)	33	47
Pacific Ocean (13)	1	2
Number of returns	87	372

* Delta sample includes only bass 15 to 24 inches long at tagging.
† Numbers in parentheses refer to recovery areas defined in Figure 1.

Suisun Bay, while only 10 of 93 returns from fish tagged in the western Delta during the spring of 1958 came from areas downstream from Suisun Bay. These early downstream recoveries could be either individuals which returned to the Bay before spawning or early spawners which migrated downstream rapidly.

From June through October 1959, fish tagged in the western Delta in the fall of 1958 migrated similarly to those tagged there in the spring of 1959. In contrast, 70% of 27 fall-tagged fish recaptured between November 1959 and March 1960 were caught in the Delta, while only 33% of comparable returns from the 1959 spring-tagged group were from the Delta. This was further evidence that the mature striped bass population was divided into rather distinct components, which could be distinguished by the nature of their migration to the Delta.

San Pablo Bay fall population.—Striped bass tagged in San Pablo Bay in the fall of 1958 averaged only 18.7 inches FL, with 61% being under 20 inches long. Since many immature females were present in San Pablo Bay at this time of year, this group, which was absent in the Delta samples, was presumably well represented in the San Pablo Bay sample.

Tagging in San Pablo Bay extended from 26 September through 13 November. All October recaptures came from areas downstream from Suisun Bay; but in November, 17 of 52 returns were from the Delta. The November through February returns of these tags differed from returns of striped bass tagged in

TABLE 12.—*Comparison of tag returns from striped bass tagged in 1950–1952 with returns from those tagged in 1958–1961*

Recovery localities[a]	June–August		September–October		November		December–February		March–May		Total percentage	
	1950–52[b]	1958–61[c]	1950–52	1958–61	1950–52	1958–61	1950–52	1958–61	1950–52	1958–61	1950–52	1958–61
Upper Sacramento River (5)	1	†	0	†	0	†	0	†	3	7	4	7
Eastern Delta (2,3, 6)	2	†	3	†	1	1	0	1	10	1	16	3
Lower Sacramento River (4)	3	1	5	2	3	1	1	1	5	2	17	7
Western San Joaquin Delta (1)	3	†	10	1	4	2	4	1	12	3	33	7
Suisun Bay (7, 8)	2	1	†	2	0	2	1	1	1	†	4	6
San Pablo area (9, 10, 11, 15)	15	6	5	9	†	3	†	2	5	1	25	21
San Francisco Bay (12)	1	17	1	11	0	3	0	8	0	2	2	41
Pacific Ocean (13)	0	5	0	2	0	†	0	†	0	†	0	7
Total percentage	26	30	24	26	9	12	6	14	35	17		
Total number	80	720	74	699	27	332	19	342	109	421	309	2,514

[a] Figures in parentheses denote recovery localities defined in Figure 1.
[b] 1950–52 figures are the percentages of total returns from striped bass 15 inches or larger tagged in the western Delta. They are primarily 1950 through 1952 returns.
[c] 1958–61 figures are average percentages of June through May returns in first year after tagging for groups tagged each spring in the western Delta.
† Denotes percentage between 0 and 0.5.

the western Delta during the spring of 1958, primarily in having a lower fraction from the Sacramento River and a higher fraction from San Pablo Bay (Table 10). In the spring of 1959, a lower percentage of returns from San Pablo Bay tags came from Delta areas and a higher percentage from downstream (Table 10). Differences in returns from the San Joaquin Delta were less than those from the Sacramento Delta. The higher returns of San Pablo Bay tags from downstream areas in winter and spring presumably reflect the failure of immature bass in the San Pablo Bay sample to migrate to the Delta.

Through the summer and fall of 1959, striped bass from the San Pablo Bay sample migrated similarly to the same sized bass tagged in the Delta in the spring of 1959 (Table 11). However, more San Pablo Bay fish returned to the Delta that fall, while more Delta fish remained in San Francisco Bay.

DISCUSSION

Changes in Migration Patterns

While the general nature of striped bass migrations found from 1958 through 1961 was similar to that described for 1950 through 1952 (Calhoun, 1952, Chadwick, 1962a), there were dramatic differences (Table 12). The primary change was the much more extended seaward migration from 1958 through 1961, when 48% of the returns came from San Francisco Bay and the Pacific Ocean, in contrast to only 2% of the 1950–52 returns. Not only did striped bass migrate farther downstream; they remained there longer. Many wintered in San Francisco Bay and some wintered in the Ocean.

New fishing methods in San Francisco Bay (Chadwick, 1962b) and in the Ocean surf increased catches there biasing these returns. This did not invalidate the conclusion that migrations have changed, as is evidenced by the 39% of the 1958–1963 San Francisco Bay returns caught by anglers fishing in areas where old fishing methods are still generally used.

As a corollary to the increased downstream migrations, striped bass did not return to the Delta until later in the fall and generally spent less time there between 1958 and 1961 than during the 1950–1952 period (Table 12).

The 1958–1961 returns from the San Joaquin Delta were much fewer in comparison with the 1950–1952 period than were the Sacramento River returns, indicating a shift in relative use of different parts of the Delta. This was most pronounced in upstream areas in the spring. Upper Sacramento spring returns increased from 3 to 7% of annual returns, while eastern San Joaquin Delta (Area 2) spring returns decreased from 10 to 1%.

While the 1962 through 1964 returns were biased by the growth of tagged fish, migrations remained generally similar to those in 1958–1961.

The 1950–52 study was the first quantitative study of adult bass migrations, there being only very limited information on earlier movements (Scofield, 1931). Party boat reports from the sport fishery (Calhoun, 1949; Chadwick, 1962b) revealed that a substantial fishery existed in San Francisco Bay from 1938 through 1943. Catches there were smaller from 1943 through 1955; after 1955 they increased rapidly to a level far higher than in any previous year. This suggested that the 1950–52 tagging study occurred during an extended period of low migration into San Francisco Bay, but that recent migrations into San Francisco Bay have been greater than those about 1940. However, the new fishing methods undoubtedly increased catches disproportionately to the number of bass migrating to the Bay.

Effects of changed migrations

These changes have decreased fishing success in the Delta and increased success in San Francisco Bay (Chadwick, 1962b). While supporting statistics are not available, observations indicated a shift in effort and success from the San Joaquin Delta to the Sacramento River.

The decrease in returns from the San Joaquin Delta and the increased returns from the upper Sacramento River during the spring suggest a change in the relative use of these areas for spawning. Data on the relative distribution of eggs and fry are insufficient to test this hypothesis. However, data on the midsummer distribution of young-of-the-year striped bass support the hypothesis. Specifically, the ratios of catches in the San Joaquin River at Antioch to catches in the Sacramento River above Collinsville averaged 1.44 from 1953 through 1957 and 1.04 from 1958 through 1962 (Chadwick, 1964).

Causes for changed migrations

Migrations were rather consistent within each period but quite different between the 1950–52 and 1958–64 periods, indicating that migration changes must have been caused by major differences in either the environment or the bass population. The present pattern may well be a reversion to earlier conditions, since catches were large in San Francisco Bay about 1940.

Some physical environmental changes, such as hydraulic changes caused by pumping water from the southern Delta into the Delta Mendota Canal, are well documented. Others, such as water quality changes associated with increasing industrial and domestic development, which was counterbalanced by improved sewage treatment facilities, are very poorly documented. Biological changes, particularly those among forage organisms, are also poorly documented. Hence it is probably impossible to determine the causes of the changed migrations.

Sufficient facts are available to suggest two contributing factors.

1) Average age of bass in the population is probably greater, since the size limit was increased from 12 to 16 inches in 1956 and commercial fishing for salmon and shad, which incidentally killed many large striped bass (Skinner, 1957), was stopped in 1957. This would contribute to migration changes since larger bass migrate farther downstream.

2) Water quality has improved in the shallow areas of San Francisco Bay as the result of improved sewage treatment. During the early 1950's, there was often no dissolved oxygen in marginal areas, but there are insufficient facts to define the extent and importance of this factor.

Factors affecting ocean migrations

Radovich (1963) concluded that the summer downstream or seaward migration of striped bass from the Sacramento–San Joaquin system is greatest when coastal sea temperatures are warm. He based this on positive correlations between mean annual ocean temperatures off central and southern California and the striped bass commercial boat catches between 1920 and 1931 and an "index of seaward migration" derived from the sport fishery in the Delta and San Francisco Bay from 1938 through 1959. Further, he hypothesized that this seaward migration extended out into the Ocean during warm years, although records of striped bass occurrence in the Ocean were insufficient to demonstrate this conclusively.

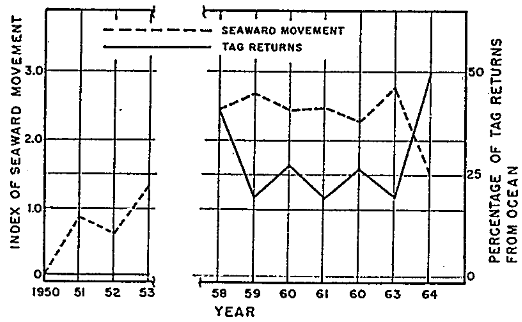

FIGURE 4.—Comparison of index of seaward movement (average daily catch per angler on party boats in upper San Francisco Bay divided by a comparable figure from the Delta) developed by Radovich (1963) and the extent of ocean migrations indicated by tag returns.

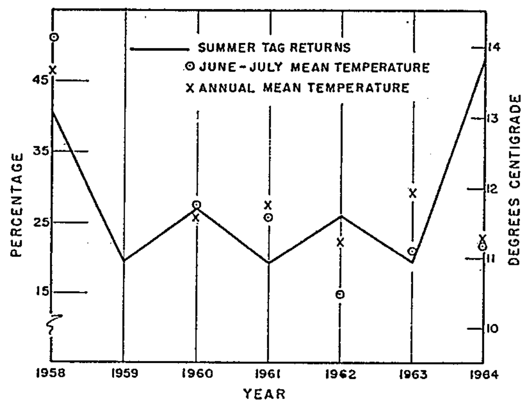

FIGURE 5.—Comparison of surface sea temperatures at the Farallon Islands, California, and the percentage of summer tag returns from striped bass 25 inches or more long which came from the Pacific Ocean.

The 1960 through 1964 "indices of seaward migration" are 2.436, 2.471, 2.284, 2.788, and 1.534 (unpublished data). Respective 1961 through 1964 mean annual sea temperatures at La Jolla and Pacific Grove are 16.5, 16.2, 17.0, and 16.7, and 13.1, 12.6, 13.4, and 12.8. Since 1956, the correlation between the index and sea temperatures has been poor, as sea temperatures have varied over almost the entire range for the 27-year period, while the index has been uniformly higher than in earlier years. As Radovich pointed out, this might be caused by new fishing methods now used in San Francisco Bay, rather than by a change in relationships.

Tag returns and Radovich's index of seaward movement both indicate a greater ocean fishery in the 1958–1964 period than in the early 1950's (Figure 4). However, from 1958 through 1964 the index and the percentage of summer tag returns from the Ocean (Figure 4) have a highly significant negative correlation ($r = -0.827$). Thus, when a large share of the bass population moves into San Francisco Bay, the index gives a poor indication of the fraction reaching the Ocean. Presumably the index is highest when striped bass concentrate most in the Bay and declines when they move through the Bay into the Ocean.

A major difficulty in interpreting the significance of the correlations between temperatures and catches is that the catch statistics are not direct measures of striped bass occurrence in the ocean. Tag returns are the only available quantitative measure of the ocean fishery. They presumably reflect the fishery quite well, but there is no way of knowing how well the fishery reflects ocean migrations.

Neither the tag returns nor recent observations of the fishery indicate a close correlation between the magnitude of the Ocean fishery and sea surface temperatures. Calhoun (1952) reported spectacular surf fishing for striped bass in 1948, and two of the few fish tagged in 1947 were caught in the Pacific Ocean that summer. However, there were no reported ocean returns from the 5,632 fish tagged in 1950, 1951, and 1952, and observations indicate very few bass were caught in the Ocean from 1949 through 1957. In 1958, ocean fishing was spectacular as far south as Monterey Bay. Every year since then, ocean catches and tag returns have been substantial.

In 1948, the mean annual sea temperature at La Jolla was the second lowest ever recorded, and the mean at Pacific Grove was below the mean of the last 45 years (Radovich, 1963). From 1948 through 1956, temperatures at both localities remained low. In 1957 they increased sharply. They peaked at La Jolla in 1958 and at Pacific Grove in 1959; since 1960 they have been comparable to low temperatures through the early 1950's.

In all recent years except 1959, surface sea temperatures are available from Farallon Islands, about 20 miles off San Francisco

(University of California, Scripps Institution of Oceanography, 1960, through 1965). These temperatures give a better measure of ocean conditions in the area utilized by striped bass than either Pacific Grove or La Jolla temperatures. The correlation coefficient for the relationship between mean annual temperatures at the Farallons and the 1958–1964 percentages of summer tag returns from striped bass 25 or more inches long that were caught in the Ocean is 0.213 (Figure 5). The comparable correlation coefficient for Pacific Grove temperatures for the same period, plus 1959, is 0.107. The correlation coefficient for the relationship between these tag returns and the June–July mean temperature at the Farallon Islands is 0.373 (Figure 5). None of these coefficients differs significantly from 0. The significance of this is reduced by the inherent variability possessed by coefficients based on such few samples and the relatively few fish (range from 59 in 1964 to 187 in 1960) on which the percentages of tag returns are based. Nevertheless, they strongly suggest that the magnitude of the Ocean fishery has not been closely related to mean annual or summer mean sea temperatures from 1958 through 1964.

Thus, the excellent ocean fishing in 1958 occurred when ocean temperatures were high, but ocean fishing was much poorer in 1957 and 1959, when temperatures were also high. In 1948 surf fishing was relatively good when temperatures were low, and ocean fishing in the early 1950's was much poorer than in the early 1960's, despite comparable temperatures. While the ocean fishery may not reflect the magnitude of ocean migrations exactly, gross differences such as those that occurred between the early 1950's and the 1958–1964 periods, almost certainly reflect substantial differences in the magnitude of ocean migrations. Since there are important discrepancies between measures of the ocean fishery and ocean temperatures, it appears reasonable to conclude that any relationship between ocean migrations and ocean temperatures is not as direct as might be inferred from the correlations Radovich described.

Many fishermen believe that striped bass runs along the ocean beaches occur most frequently when tidal fluctuations are greatest. To test this hypothesis, summer catch rates for tagged striped bass in the ocean were compared for days when tidal fluctuations were great (lower low tide below mean sea level at the Golden Gate) and days when tidal fluctuations were smaller than this. In 1959 the catch rate was about 3% higher on days with small tidal fluctuations. In other years it was higher on days with large fluctuations, with the respective annual percentage differences being about 2, 11, 14, 17, and 100. Thus, if a real difference exists, it is apparently slight in most years.

Comparisons with migrations elsewhere

Striped bass migrations described in Coos Bay, Oregon (Morgan and Gerlach, 1950) are similar to migrations in the Sacramento–San Joaquin system.

Migrations of Atlantic Coast striped bass populations are more complex. These populations are noted for extensive ocean migrations up the coast in the summer and back in the fall. However, published evidence indicates ocean migrations are largely supported by Chesapeake Bay area stocks (Raney, 1952). The few large fish tagged in Chesapeake Bay and North Carolina (Chapoton and Sykes, 1961) participated in this ocean migration but otherwise migrated similarly to comparable sized fish in California.

Smaller striped bass, which comprise the bulk of fish tagged in Chesapeake Bay, seldom participate in the ocean migration (Mansueti, 1961). These fish have migrations generally similar to the larger striped bass tagged in the early 1950's in California (Massmann and Pacheco, 1961). However, their migrations are apparently more diffuse, and they do not regularly migrate as far downstream (Mansueti, 1961) as larger California striped bass have recently. Similarly, smaller striped bass from other Atlantic Coast populations apparently migrate only short distances from their parent river systems (Raney, 1952; Raney, Woolcott and Mehring, 1954).

Few large striped bass have been tagged in Atlantic Coast estuaries other than Chesapeake Bay, so no general comparison can be made between migrations of large California striped bass described in this paper and similar populations on the Atlantic Coast.

Mansueti (1961) observed that 6 of 8 bass tagged in Chesapeake Bay tributaries during the spawning season and recaptured during subsequent spawning seasons were caught near the tagging site—additional evidence of homing to spawning sites.

SUMMARY

Migrations of striped bass in the Sacramento–San Joaquin River system, California, were studied from 1958 through 1964. Most conclusions are based on tag returns from mature bass tagged in the western Delta during their spring spawning migration. Some conclusions are based on tag returns from other groups of tagged bass and from observations of angler catches.

Striped bass tagged at different locations in the western Delta and at different times during the spring migrated similarly. The only important difference was that those tagged in the San Joaquin portion of the Delta tended to return there the next year.

Larger mature fish migrated farther downstream than smaller ones. Mature males and females in the same size groups migrated similarly.

Immature males and females do not participate in the spawning migration to the Delta. Since females mature at a greater age than males, they dominate Bay area catches in the spring, while males dominate catches in the Delta. Males probably remain on the spawning grounds longer than do females, further contributing to these disproportionate sex ratios.

Striped bass tagged in the western Delta in the spring migrated to salt water in the late spring. In summer the population was generally centered in San Francisco Bay, but substantial numbers were caught in the Pacific Ocean from Tomales Bay to Monterey. They started returning to the Delta in the fall, but many wintered in the Bay area. During the spring most were in the Delta or upper Sacramento River and its tributaries. There were appreciable annual variations in these migration patterns.

Striped bass tagged in the upper Sacramento River and eastern Delta in the spring and in the western Delta during the fall migrated similarly to bass tagged in the western Delta in the spring. In each case the major difference was that migrations to the Delta were distinctive, with bass tending to return to the tagging area a year following tagging. This indicates that the population is divided into components with somewhat different migrations. The same phenomenon has been noted in Chesapeake Bay.

Fish tagged in the fall in San Pablo Bay also migrated similarly. However, many of them remained in the Bay area the following spring, presumably because they were immature.

The migration pattern from 1958 to 1964 was generally similar to that in the early 1950's. However, there were two major differences. The most important was that in the later period bass generally migrated farther downstream and stayed there longer. The second was a shift from the San Joaquin to the Sacramento side of the Delta in the later period. As a result, striped bass fishing in San Francisco Bay and the Pacific Ocean was generally better, while fishing in the Delta was generally poorer, in the later period. Also, the importance of the Sacramento River as a spawning area may have increased.

There have been some important changes in the environment and the striped bass population which could cause these changes in migrations. However, few quantitative data about these changes are available, so no definite conclusions about causes could be reached.

Observations of the fishery and tag returns suggest that the magnitude of migrations to the Pacific Ocean is not as closely correlated with ocean temperatures as earlier studies had suggested.

Migrations in the 1958–64 period are similar to migrations reported from Oregon. They differ from Chesapeake Bay stocks in that many Chesapeake Bay fish undertake longer ocean migrations. However, migrations of small bass from other Atlantic Coast subpopulations are more restricted than those for small bass from Chesapeake Bay, so the migrations of large bass from other sub-

populations may be more similar to migrations in the Sacramento–San Joaquin system. This could not be confirmed, since data on migrations of larger bass in these populations are lacking.

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